BIOLOGY OF ELEONORA'S FALCON (FALCO ELEONORAE): 1. INDIVIDUAL AND SOCIAL DEFENSE BEHAVIOR

by
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Abstract

Most Eleonora's Falcons breed colonially on some small islands in the Mediterranean Sea. Falconiformes, owls, and crows, but not gulls are attacked socially and effectively warded off. Such mobbing occurs outside the limits of breeding territories. Ground predators, on the other hand, are attacked by individual falcons rather than by social mobbing, although this group of predators causes the major losses of falcon broods.

Introduction

Species of the genus Falco that are solitary are generally territorial and attack potential predators near their nest (Brown and Amadon 1968). Certainly, this is also true for Eleonora's Falcon (Falco eleonorae), but as a consequence of its colonial breeding, social mobbing can be observed (Mayol 1977, Walter 1978, 1979). Sociality in this falcon does not seem to be highly advanced as compared to other social animals and therefore, they offer an opportunity to study one stage in the evolution of social behavior. In this report, we describe social mobbing and its limitations by territoriality. We distinguish aerial predators as those that can fly and which are usually encountered outside the individual breeding territories, and ground predators as those inside the territories as potential predators of eggs or young falcons.

Materials and Methods

We visited a falcon colony in the Aegean sea on 5 expeditions from 1965 to 1977 and spent a total of 5½ months there during the breeding seasons. Our observations covered the interval from the first week of July to the middle of October. The colony was situated on an uninhabitated island approximately 0.5 by 1.0 km in size and about 20 km from the nearest large island. There were about 180 pairs of falcons each year. As we lived in a cave in the midst of the breeding territories, we were aware of events almost continuously and re-orded every encounter with intruders on the colony. Encounters with harmless species such as hares and lizards were recorded. Experiments with stuffed birds, rats, plastic snakes, and a plastic kite bearing the silhouette of an eagle were conducted. These experiments were carried out after the chicks were at least 10 days old.

Results

Defense against aerial predators

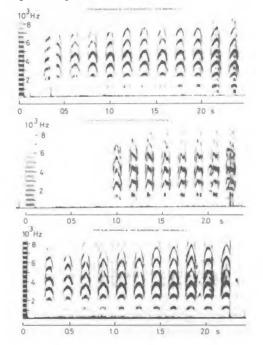
During the autumn breeding season, potential predators such as other raptors or crows approach the falcon colony on migration. In such situations, a fright call is sometimes given once or twice (a shrieking "kraiere" with the accent on "i"). At the same in-

stant the falcons leave their nests or resting sites and start to give intensive excitation or alarm calls, like a nagging "yek-yek-yek...," in males pitched higher than in females (Fig. 1). The island size and the noise of wind and sea make it difficult to quantify the use of the fright call. We have the impression that when it is used, more than 100 falcons join in mobbing; when it has not been used and only excitation calls are given, about 20 to 50 falcons attack. Falcons, calling excitedly, gathered above the predator and individuals repeatedly dived from 5 to 10 m behind it, aiming at the shoulder. Although a direct hit was observed only once (in the case of a Short-Eared Owl, Asio flammeus), the mobbed bird attempted to evade the attacks and flew away from the island. There seems to be no difference in the intensity of mobbing when the falcons had eggs or chicks.

In three experiments with a plastic kite (eagle silhouette) about 12 falcons gathered above it, as soon as it was more than 20 m from the ground. They did not call, but performed several stoops, and soon lost interest.

A striking change in behavior was observed when, in spite of the mobbing group, a Steppe Eagle (Aquila rapax) landed inside the territory of a pair of falcons with young

Figure 1.-Sonagram of excitation call of Eleonora's Falcon; 80-8000 Hz, bandwidth 300 Hz.



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- a) Male voice. Notice the slight increase of frequency with time; the increase in intensity is most pronounced for the fundamental frequency and the uppermost harmonics. The female enters synchronously for the last three calls shown, the call being deeper and shorter. For other female individuals the call can have the same length and the same fundamental frequency as the call of this male. However, for females the relative intensity of the fundamental frequency as compared to the harmonics is always greater than for males.
- b) Excitation call of another male. Notice the higher frequency and the varied pattern as compared to a). Again the female enters for the last two calls shown.

c) Female call.(A sound recording of the fright call is not available.) about 10 days old. The other falcons retreated to their own territories and only this pair and the neighboring pair continued their excitation calls and attacks. When the eagle took flight, it again elicited the usual mobbing response.

The impression that social mobbing occurs outside of the individual nest territories was supported by the following experiment. A stuffed Carrion Crow (Corvus corone) was placed in turn near 10 nests with chicks. At 9 nests it produced no obvious response from the adults. At the tenth nest, the female started calling excitedly a few seconds after the dummy had been put down, flew towards it almost horizontally, hit it on the shoulder with its talons during flight, flew in a circle and hit it again. Then it hovered 5 m above the crow, dived vertically to about 1 m from the crow and soared up. This behavior is similar to that of the Peregrine Falcon (Falco peregrinus) and Merlin (Falco columbarius) towards possible terrestrial predators (Brown and Amadon, 1968). The excited female did not evoke any response from other pairs. Even the male rested and called only occasionally while the female pounced onto the dummy every 10-20 seconds. It made no difference whether the crow was placed at this nest or 10 m away still within this female's territory. The attacks were continued after the crow had been knocked over. After its removal, the female sat in the territory, often at the nest, and kept calling for another 15-20 min. The fright call was not heard under these conditions, and no response to other dummies could be obtained prior to or after experience with the crow. When we repeated the experiment 1 week later, the crow was again singled out.

The behavior towards other possible predators of eggs or young is not so overt. Other falcon species, herons, and gulls (see Table 1) are allowed to land on the island provided they stay about 50 m away from the nearest nest. However, 20 to 50 m is the usual size of the radius of the nesting territory (see Walter 1979). When they landed closer to a

Table 1. Frequency (during 5½ months) of possible aerial predators closer than 1 km to the colony of Eleonora's Falcon, compared to the frequency of defensive behavior by falcons.

	Total observations	Individual defense response	Social mobbing
Accipitridae Strigidae Corvidae	231	0	22
Falconidae	132	4	2
Ardeidae	153	2	0
Laridae	>5004	2	0

¹Aquila rapax, A. clanga, A. pomarina, Hieraaetus fasciatus, H. pennatus, Milvus migrans, Circus aeruginosus, Circaetus gallicus; Asio flammeus; Corvus corax

²Falco peregrinus, F. tinnunculus, F. naumanni. In addition to these observations a dead F. tinnunculus was found on the island and a F. naumanni was fed to chicks.

^aArdea cinerea, A. purpurea, Egretta garzetta, Ardeola ralloides, Bubulcus ibis, Nycticorax nycticorax

Larus argentatus, L. audouinii

nest, single pairs or individuals attacked them with or without excitation calls. Individual attacks on gulls in a Moroccan colony (Clark 1974) seem to be more frequent than in the Aegean colony we studied.

A stuffed Herring Gull (Larus argentatus) placed in turn near 10 nests elicited no reactions from the falcons. Even a pair that had attacked a gull in flight near their terri-

tory did not respond to the dummy near their nest.

About 1% of the falcon broods are lost accidentally to Cory's Shearwater (*Calonectris diomedea*) when the falcon's nest is in the entrance of a shearwater's crevice. However, adult shearwaters passing close to the island are only on exceptions chased for a few seconds by a single falcon. Apart from such accidents, no eggs, young or adult falcons were lost to aerial predators.

Defense against terrestrial predators

To understand the limits of social defense behavior, we briefly describe the behavior against possible ground predators. Such predators include man, rats, and to a lesser extent, snakes.

Eggs are sometimes taken by egg collectors, while young falcons are taken by hunters and local fishermen to eat as a delicacy. When we approached a territory, no mobbing by a group of falcons was elicited. Individual birds behaved as follows: As long as only eggs were present, the incubating falcon (usually the female) flew off and circled 5-40 m above the site. After the young had hatched, the female also gave excitation calls. The older the young, the more intensive the call, especially when young began to scream. Circling was interrupted by occasional raids at the intruder but without it being hit. Neighbors did not join the pair in defense, although toward the end of the breeding season falcons came to circle and call together when we appeared, but they soon lost interest. Three goats (Capra hircus) living on the island during 2 seasons were treated in the same way as human beings only once. Hares (Lepus capensis) were never molested.

Trapping and banding alerted the falcons, but otherwise they did not respond to the threat of being caught and they never screamed while handled. One pair was caught repeatedly in the same and in different seasons, both when they had eggs as well as when they had 2 weeks old chicks. No increase in defensive reaction of either partner was noticed when we entered their territory repeatedly. This was also true for the 20+ pairs where one member was trapped while the remaining bird watched.

Density of rats (Rattus rattus) on the island varies from year to year, but appears to be constantly high, for we caught 5 rats in a single night with 1 trap. About 20% of falcons' eggs are destroyed by rats (Wink et al., 1979). Although rats prowled in the shade as early as late afternoon, we did not observe predatory or defensive behavior by falcons toward rats, nor did we hear conspicuous falcon calls during the night that would sugest predation. Lizards (Lacerta erhardii) are usually tolerated and may creep under the female's wing and tail in search of ectoparasites or sunbathe on her tail. They are sometimes caught and killed, but not eaten. Dried lizard carcasses were found in about every 15th nest. Rat carcasses were absent from nests. No defense response was elicited in experiments with a stuffed rat.

A snake has been vigorously attacked in a Moroccan colony (Clark 1974). No snakes were on the island we studied, so we could only test the falcon's response by pulling a plastic snake with a piece of string close to a nest with female and chicks. The bird flew off without calling. Placing the dummy at other nests had no obvious effect.

Discussion

How can we explain that Eleonora's Falcons have such an effective defensive mobbing behavior against aerial predators, but do not show similar response to rats feeding on unattended eggs? We assume that rats appeared only recently on the island and that specific reactions have not yet evolved. The falcons' indifference to being caught by us reminds us of other species on islands without terrestrial predators, for example, the Galapagos Islands.

Mobbing has been studied in various birds (Shalter 1978) and is most prominent in colonial species. Social mobbing in the case of Eleonora's Falcon is similar but the situation is more complicated than for terns (Sterna sp.) or bank swallows (Riparia riparia) (Hoogland and Sherman, 1976). Although the Eleonora's Falcon breed colonially, they nevertheless have individual territories similar to solitary breeding falcons in which neighbors are not tolerated (Walter 1978). Social mobbing is limited by this behavior: as soon as an aerial predator is within a territory, social reaction ends and only individual attack continues. This seems to be true for ground predators as well. Individual attack is comparable with that of solitary falcons and is effective considering the size of Eleonora's Falcon (female weight 390 g).

We assume that due to ecological adaptation, Eleonora's Falcon developed from a solitary species to a colonial species. Originally, predators may have been deterred by the individual action of several falcons. When selection pressure from the presence of predators (the autumn breeding season coincides with the increased number of raptors passing on migration) is the same or higher as compared to a solitary falcon (Table 1), then defense could improve by changing to social mobbing. We suggest that important components of social behavior are the stimulating effect of fright calls and possibly the excitation call. Finally, there is the effectiveness of social mobbing. It is difficult to quantify the degree of sociality reached so far in tis species. An effective way to test advantage of social mobbing would be to establish a correlation between colony size and effectiveness as has been done for bank swallows (Hoogland and Sherman, 1976).

Acknowledgments

We thank the Institut für Vogelforschung, Vogelwarte Helgoland, Wilhelmshaven and the Naturwissen-schaftliche Museum Coburg for supplying stuffed bird dummies, and we are grateful to Dr. H. Goydke/Physikalisch Technische Bundesanstalt, Braunschweig for making sonagrams. Ms. A. Koehler/Freiburg and Prof. M. Edmunds/Preston kindly commented on an earlier draft of the manuscript. Finally we thank our friends in Greece for their help and interest during our studies.

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Part 1 of a series on Eleonora's Falcon.



Description of Photo— Nest defense: Female Eleonora's Falcon hits a stuffed Carrion Crow placed at falcon nest. (see p. 67).